



MCZ  
LIBRARY

FEB 21 1989

HARVARD  
LIBRARY

Volume 21 Number 16 pp. 259-273

15 February 1989

TRANSACTIONS  
OF THE SAN DIEGO  
SOCIETY OF  
NATURAL HISTORY

## A new abyssal hydrothermal verrucomorphan (Cirripedia; Sessilia): The most primitive living sessile barnacle\*

William A. Newman and Robert R. Hessler

*Scripps Institution of Oceanography A-002, La Jolla, California 92093 and Natural History Museum, P.O. Box 1390, San Diego, California 92112 USA*

*Abstract.* A remarkable sessile barnacle, *Neoverruca brachylepadoformis* gen. et sp. nov., has been discovered living near abyssal hydrothermal vents at 3600 m in the Mariana Back-Arc Basin, Western Pacific. It has closer affinities with the earliest known sessile barnacles, the Brachylepadoomorpha (?Upper Jurassic–Miocene), than with any of the fossil or extant Balanomorpha (Upper Cretaceous–Holocene). Thus *Neoverruca*, the most primitive living sessile barnacle, is a “living fossil.” However, there are subtle characteristics of its shell that are diagnostic of the asymmetrical sessile barnacles, suborder Verrucomorpha (?Middle, Upper Cretaceous–Holocene). In having verrucomorphan specialization superimposed on the brachylepadoomorphan plan, *Neoverruca* constitutes a “missing link” between these two suborders. As the sole surviving member of an ancient radiation, *Neoverruca* adds significantly to our knowledge of the origin and evolution of sessile barnacles and the nature of their pedunculate ancestor. Furthermore, it heightens our appreciation of the role abyssal hydrothermal environments play in perpetuating ancient forms whose wide-ranging, predominantly shallow-water ancestors have long been extinct.

### INTRODUCTION

A little more than a decade ago communities of large clams, mussels, tube worms, and other animals were discovered at depths of 2600 m or so, clustered around abyssal hydrothermal vents of the Eastern Pacific, near the Galapagos Islands and at 21°N off Mexico (Hessler and Smithey 1983, Jones 1985). The latter locality provided the first vent barnacle, *Neolepas zevinae* (see Newman 1979), and <sup>18</sup>O determinations subsequently confirmed that it was living in waters several degrees above ambient (Killingley and Newman 1982).

*Neolepas*, a well-armored form having an apparent fossil record dating from the ?Lower Jurassic of New Caledonia (Buckeridge and Grant-Mackie 1985), is the most primitive living scalpelloid and the sole surviving member of the Eoscalpellidae (Lower Triassic; Buckeridge 1983). Other than its primitive arrangement of capitular plates, *Neolepas* is specialized in having appendages that differ from those of all shallow-water as well as deep-sea scalpelloids in being adapted for feeding on extremely fine suspended material transported by gentle currents (Newman 1979).

Additional populations of the same species of *Neolepas* were subsequently discovered by French scientists at the same depth from 13°N off Mexico (Newman 1985). However, although recruitment on artificial substrates placed in the area has been conspicuous (C. van Dover, *personal communication*), all collections have yielded little more than a dozen adult specimens. Therefore, while *Neolepas* is evidently endemic to hydrothermal vents in the East Pacific, it is a relatively inconspicuous member of the communities found there.

The new form, *Neoverruca brachylepadoformis* gen. et sp. nov., differs from *Neolepas* not only in being sessile but in being one of the most abundant and conspicuous

\* Contribution of the Scripps Institution of Oceanography, new series.

members of the macro-fauna of the hydrothermal vents at 3600 m in the Mariana Back-Arc Basin, Western Pacific, and this fauna differs in other ways from those seen in the Eastern Pacific (*see* Hessler *et al.* 1988). Nonetheless, *Neoverruca* is ecologically similar to *Neolepas* in being completely armored and provided with delicate appendages adapted for feeding on very fine material transported by gentle currents (*see* Anderson 1980 and Zevina 1988, and Anderson and Southward 1987, concerning feeding in *Verruca* and cirripeds in general, respectively).

*Neolepas* and *Neoverruca* are the most primitive living members of their suborders, the Scalpellomorpha and Verrucomorpha, respectively, both of which first appear in the Mesozoic. Thus, these genera are relics<sup>1</sup> surviving in the refugia provided by abyssal hydrothermal springs long after their less specialized Mesozoic ancestors went extinct.

#### DESCRIPTION

##### Suborder Verrucomorpha Pilsbry, 1916, U. Mesozoic–Recent

(For an amendment of the suborder and a proposal for new families within it, *see* the systematic section below.)

##### *Neoverruca* Newman, gen. nov.

*Diagnosis.*—Verrucomorpha (*see* systematic section below) having several whorls of small, imbricating plates surrounding the base and elevating the wall above substratum, and with a median latus interposed between scutum and tergum of the movable side. Type: *Neoverruca brachylepadoformis*. Etymology: A new (*neo*, G.) wart (*verruca*, L.).

##### *Neoverruca brachylepadoformis* Newman, sp. nov.

Figures 1, 2, 3, and 4C-1

*Diagnosis.*—As for the genus, although the median latus becomes rudimentary with growth and may be completely corroded away in old individuals. The scuta have internal, apical teeth; the appendages are modified for feeding on extremely fine particles (*see* Newman 1979), and there is a median-dorsal filamentary appendage and a pair of ovigerous fraena, but caudal appendages are absent. Etymology: Short-shellfish (*brachylepas*, G.) form (*form*, L.).

*Material.*—More than 100 adult hermaphrodites and 12 or so juvenile stages attached to ferriferous crusts and vent mussels near hydrothermal springs of the Mariana Back-Arc Basin in the Western Pacific (18°12'N; 144°42'E) at depths of approximately 3600 m. ALVIN Dives (Stations) 1822, 1840, and 1844, April 1987. Temperature field from 5 to 15°C (Hessler *et al.* 1988).

*Deposition of types.*—Holotype U.S. National Museum of Natural History Cat. no. 240030, and two paratypes to each of the following institutions: USNM Cat. no. 240031; British Museum (Nat. Hist.) Reg. no. 88.274-275; National Museum Nat. Hist. Paris, Ci 2050; University of Auckland; Zool. Mus. Copenhagen; Zool. Mus. Moscow State University; National Sci. Mus., Tokyo.

*Hard parts.*—Asymmetry of the shell in verrucomorphs involves ontogenetic changes in the proportions and the arrangement of the plates, and individuals can be either right or left sided. For ease of description and discussion both sides are illustrated as though they were right sides (except in Fig. 2) and identified as follows: The side supporting the movable tergum and scutum (operculum), and where the rostrum and carina come in contact, will be called the “movable side.” The opposite side, where the gap between the rostrum and carina is filled by the fixed scutum and tergum, will be called the “fixed side.”

<sup>1</sup> The term “relic” is used here to specify a survivor of an ancient lineage, in contrast to a “relict” or subpopulation isolated from a parent population by some vicariance event (*see* Udvardy 1969:208 for discussion).

These designations, "movable and fixed sides," apply to all verrucomorphans and distinguish their unique morphology from that of the symmetrical sessile barnacles. However, if a specimen of *Neoverruca brachylepadoformis* were viewed from one side or the other, while the nature of the opposite side remained unknown, it would be diagnosed as a brachylepadomorphan. Furthermore, without the more detailed information on and illustrations of the opercular parts and wall presented here, it would be difficult to decide if a mixed sample of disarticulated plates from several individuals of this species represented a neoverrucid or a brachylepadomorphan, as was the case with a number of fossil shell lots assigned by Darwin to a pedunculate barnacle, *Policipes*, before Withers (1914a) recognized them as a new and primitive brachylepadomorphan, *Pycnolepas*. Thus, it is possible that some fossils considered brachylepadomorphans may actually represent neoverrucids.

The movable side, supporting the movable scutum and tergum, tends to be flattened or slightly concave in the vertical plane, while the fixed side is somewhat rounded. Depending on the circumstances under which an individual grew, the scuta and terga may tilt from essentially vertical, as in *Altiverruca*, toward the fixed side, as in *Verruca*. There is no obvious shortening of the fixed scutum and tergum relative to the movable scutum and tergum in tilted individuals of *Neoverruca*, although the tilt can approach 80° in crowded individuals, bringing the plane of the scuta and terga nearly parallel to the substratum.

There are usually four whorls of relatively small imbricating plates discernible on the movable side and two or three on the fixed side of the animal. In *Brachylepas* (see Newman 1987 and Zullo *et al.* 1987), and perhaps in most *Pycnolepas* (J. S. H. Collins, *personal communication*), there are more whorls of plates, and the plates of the lower whorls possess mortises that interlock with tenons in plates of alternate lower whorls. When viewed from within, or when disarticulated, no interlocking between imbricating plates can be observed in *Neoverruca*; to the contrary, there appears to be a tendency for some plates of the lowermost whorl to be lost with growth and age.

At the rostral and carinal ends of the shell, the height the latera extend up the wall diminishes. There is a subrostral and subcarinal tier of plates, and between them there appear to be 10 to 12 tiers of latera on the movable side and 6 to 7 tiers on the fixed side. Thus there are apparently as many as 18 vertical tiers of imbricating plates around the circumference of the wall, standing two to four whorls high and supporting the principal wall plates above the substratum. This is about the number of tiers encountered in *Chionelasmus* and in the basic shell of *Catophragnus*. On the other hand, it is about half the number of tiers estimated for the highly derived interlocking imbricating plates of *Brachylepas cretacea* (see Newman 1987).

The individual plates of the imbricating basal whorls in *Neoverruca* have much the same shape and ornamentation: Each is a more or less equilateral triangle with a generally faint, narrow median ridge flanked on either side by fine striations that radiate from the apex to the base. The median tier of latera, below the median latus, covers the rostro-carinal suture on the movable side. But it takes several tiers of latera to cover the suture between the scutum and tergum, and the adjacent sutures between them and the rostrum and carina, on the fixed side (see Figs. 1A and B, 2B, and 4C-1).

The apically acute median latus, interposed between the movable scutum and tergum, becomes rudimentary, badly corroded, and weakly attached with age, and it may be lost in older individuals (see Figs. 4C-1 and 2B). A median latus in this position is unknown in other sessile barnacles except brachylepadomorphans.

Attempts to identify individual latera in adults were confusing. Part of the confusion arose because some of the marginal imbricating plates are easily lost. But the full extent of the confusion was not understood until the ontogeny of a number of the post-cyprid metamorphic stages was studied (Newman 1989). Some information on the remarkable juveniles of *Neoverruca* is given below, under "Juvenile Stages," but determination of homologies and identification of the principal latera, based on the ontogenetic analysis, are beyond the scope of this species description and will be published separately (Newman 1989).

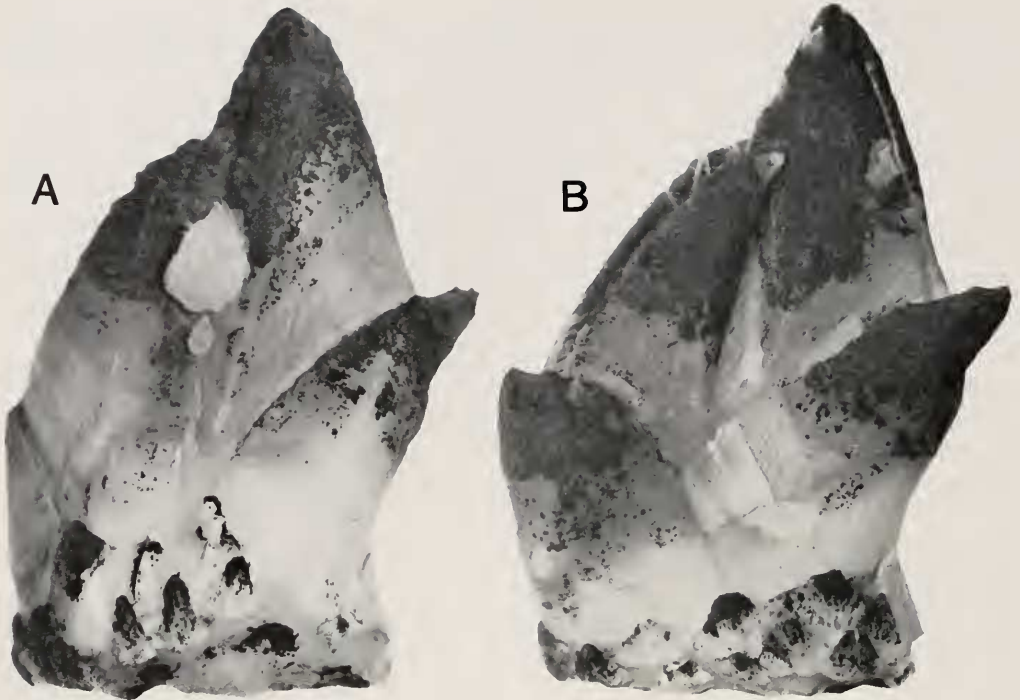


FIGURE 1. *Neoverruca brachylepadoformis* gen. et sp. nov. Large individual (2.1 cm high) from a closely packed aggregation at ALV Sta. 1843. For ease of comparison, both sides appear as right sides. Note lack of ferromanganese deposits on younger portions of shell of the adult and on the two juvenile individuals in A. See Figure 4C-1 for the form of an adult growing under uncrowded conditions (please consult Fig. 2 for identification of plates and the caption of Fig. 4 for symbols).

A, view of the fixed (FS-FT) side. Note that R and C are moderately separated, with S and T immovably fixed between them. The two recently settled juveniles both with movable (MS-MT) sides outward, first attached themselves in the depression formed by the articulation between FS and FT. It can be observed that the lower, younger juvenile appears to be basally narrower; it is a pedunculate stage with naked peduncle and typical scalpellomorphan capitulum having a relatively narrow carina and rostrum. The upper, older juvenile has undergone metamorphosis into the sessile mode, and it has added several more whorls of imbricating plates to the expanded basal margin of its capitulum.

B, view of the movable (MS-MT) side. Note that R overlaps C and that the relatively narrow S and T form a movable operculum. The median latus (L), visible on the MS-MT side of the juveniles (Fig. 1A) and the uncrowded adult (Fig. 4C-1; MS-MT), becomes vestigial with growth and, owing to corrosion, may completely disappear in large adults as it almost has here (see Fig. 2B).

The basis is membranous. When individuals are severely crowded, the basis can elongate to the extent that, when individuals are separated, some resemble pedunculate barnacles. The elongation may also include the lower portion of the wall, causing some of the lowermost plates of the imbricating whorls to separate from each other, furthering a pedunculate semblance. Elongation of bases, both membranous and calcareous, occurs in a number of distantly related sessile barnacles for a variety of adaptive reasons that include crowding. We consider elongation of the basis in *Neoverruca*, in response to crowding, to be without phylogenetic significance.

The scuta and terga are weakly ornamented, the terga by a more or less median ridge and fine longitudinal ribs or striations radiating from the apex, the scuta similarly but without a median ridge. The scutum and tergum of the fixed side are proportionately wider than their movable counterparts (see Fig. 2C, D and E, F, respectively). The movable pair fit within the confines of the margins of the fixed pair, and the scutum forms the basal hinge line high up on the lateral portions of the rostrum and carina.

The rostral angle of the fixed scutum is rolled inward (Fig. 2C) to form a condyle with the relieved rostral angle of the movable scutum (Fig. 2E). The interior of the apical region in both scuta, above the deep depressions for the scutal adductor muscle, is thickened; the thickening of the fixed scutum is produced into a short, longitudinal,

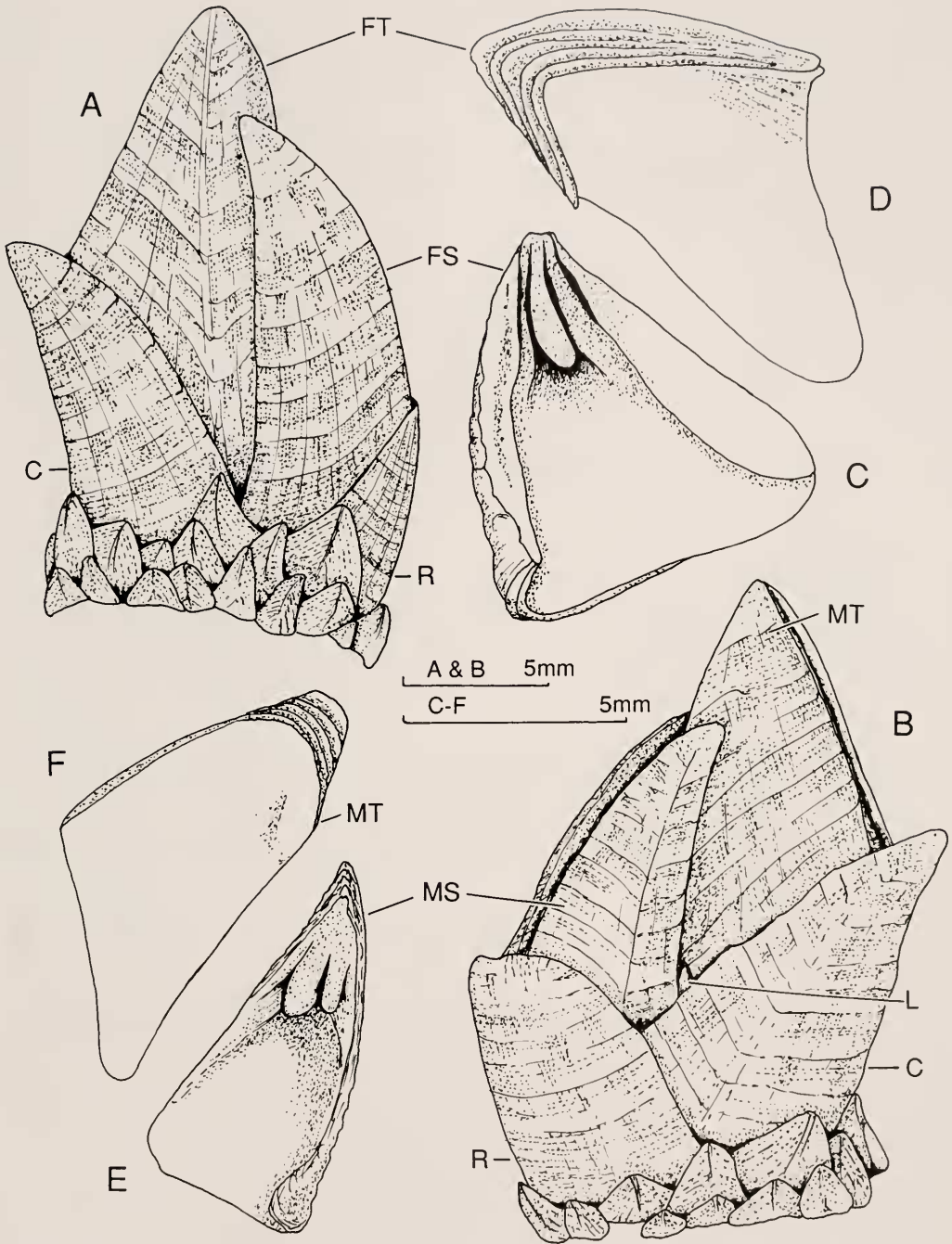


FIGURE 2. *Neoverruca brachylepadoformis* gen. et sp. nov. (ALV Sta. 1843). A and B, adult viewed from the left (fixed) and right (movable) sides, respectively. C and D, and E and F, interior views of FS and FT, and MS and MT, respectively, but from a slightly smaller individual. Note narrowness of MS and MT (E and F), as compared to those of the fixed side (C and D), and the unusual tooth-like structures in the apices of the scuta (C and E). Also note contact between R and C, and vestigial L between MS and MT, on the movable side (B).

depending tooth or ridge that comes to rest just over, or on, one or two similarly formed ridges on the movable scutum. These ridges, the condyle, and the fit along the occludent margins of the movable pair within the fixed pair assure alignment of the operculum with the wall and lock it in place when closed. The relationship of the scutal adductor

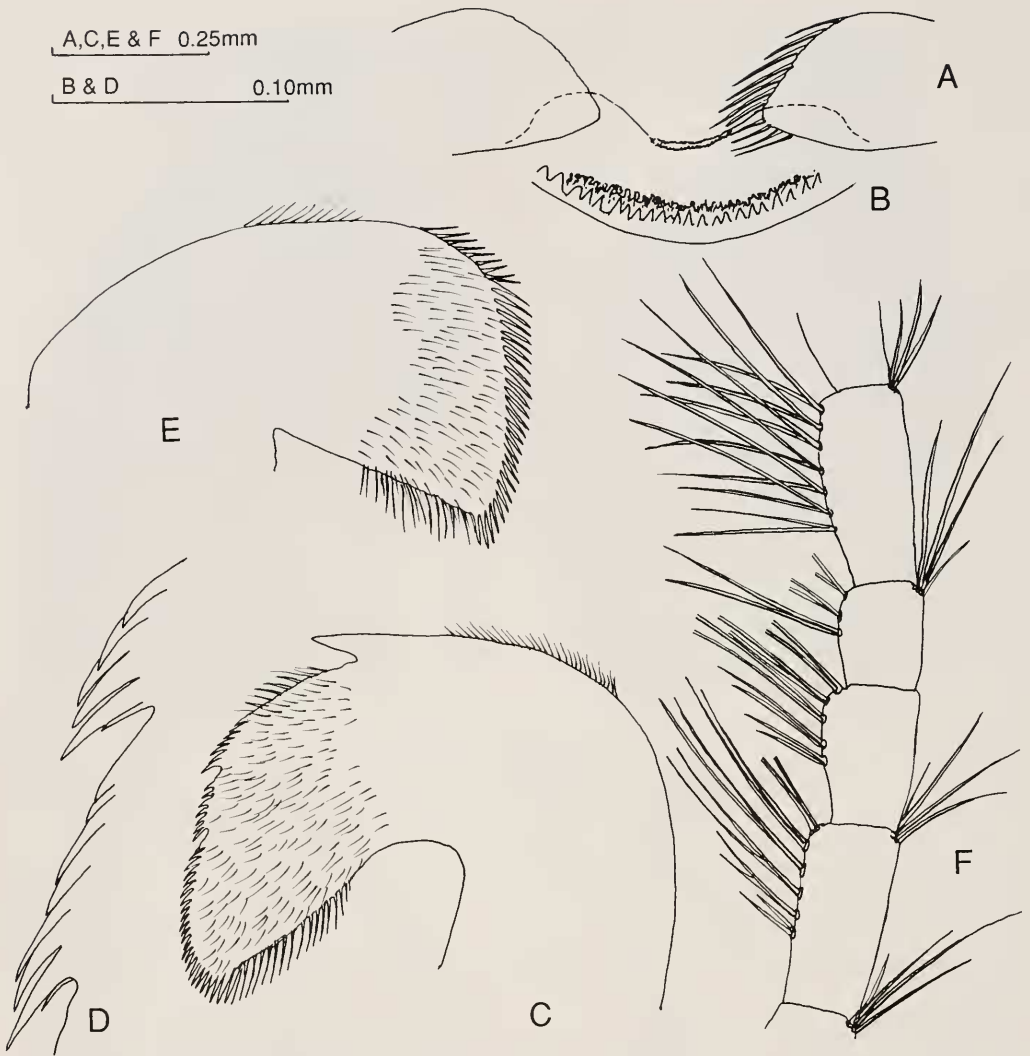


FIGURE 3. *Neoverruca brachylepadiformis* gen. et sp. nov. (ALV Sta. 1843). A, labrum flanked by mandibular palps, setae on left palp deleted; B, crest of labrum enlarged; C, mandible; D, spines of second and third tooth enlarged; E, first maxilla; and F, intermediate articles of sixth cirrus (some setae truncated to simplify illustration) (note the two anomalously short articles between the two normal ones).

muscle to these ridges has not been examined, and therefore some apodemal properties of the latter cannot be discounted, but these ridges and associated depressions are internal and are not involved with housing complementary males. The articular margins between the scutum and tergum of each side lack the well-developed articular ridges and furrows seen in some scalpelloids, most verrucomorphans, and virtually all balanomorphans.

The rostrum and the carina, also marked by fine ribs or striations that radiate from apex to base, are slightly asymmetrical and perceptibly flat on the movable side. The flattened condition could aid in their identification as "neoverrucid" when disarticulated. The carina is generally but not necessarily higher than the rostrum. Like the rostrum, it has shallow depressions around its perimeter marking the positions of the vertical tiers of imbricating plates, but the depressions are not as pronounced or arranged in as precise a manner as in *Brachylepas cretacea*. The carina also has an "alar" furrow or depression on the movable side that superficially appears to have been formed in response to overlap by the rostrum, but when an articulated specimen is

viewed from within, it is seen to accommodate the carinal portions of lower latera. Overlap between the rostrum and carina, established during ontogeny, is apparently never marked; it is the lower latera that provide protection and strength to this suture. Concomitantly, there is also a broad but shallow furrow on the carinal margin of the rostrum to accommodate them.

The lateral margins of the rostrum and carina on the fixed side are provided with narrow, smooth, articular surfaces to receive the corresponding margin of the scutum and the basi-carinal margin of the tergum, respectively. A large *latus* tends to overlap the rostro-scutal, scuto-tergal, and tergo-carinal sutures. But, for strength and protection of the more numerous sutures found on the fixed side, there are more tiers of imbricating latera than on the movable side. On the other hand, the movable side tends to have more whorls than the fixed side, especially in very young individuals that are bent over.

*Soft parts.*—The prosoma (cephalic region supporting mouth parts) is uninflated and blends imperceptibly into the thorax, as in *Verruca*. However, it bears an anteriorly directed, median dorsal filamentary appendage containing ramifications of the testes. The mouthparts are very similar to those of the hydrothermal scalpelloid *Neolepas*: The labrum is slightly bullate; the crest is concave, without a notch, and supports a single row of fine, sharp teeth behind a row of debris-laden bristles, and the palps are relatively small (Fig. 3A, B). The mandibles are clothed with fine setae, and the cutting edge consists of one strong superior spine and three low, broad teeth each supporting a single row of fine, sharp spines along their superior margins. The fourth tooth blends almost imperceptibly into the spiny lower margin, and the inferior angle is produced into a fine-toothed comb of similar spines that change to fine, soft spines along the inferior margin (Fig. 3C). The first, and second (not illustrated), pair of maxillae each have a straight cutting edge supporting a comb of fine setae (Fig. 3E). Behind the second maxillae, a subesophageal salivary gland apparently opens on a prominent median papilla.

The first two pairs of cirri are modified as maxillipeds; the rami of the first pair have inflated, heavily setose proximal articles and subequal, antenniform distal articles, and they have about 25 articles each; the second pair are similar in appearance but their rami, of about 14 and 34 articles each, are markedly unequal. The remaining four pairs of cirri are ctenopod (Fig. 3F) and have long, slender rami of about 52, 70, 84, and 75 articles per ramus, respectively; the proximal articles are wider than long and support one or two pairs of setae, while the distal articles are three times as long as wide and support as many as eight pairs of setae along the lesser curvature (Fig. 3F). The probosciform penis is as long as the posterior cirri, and caudal appendages are absent.

Approximately 100 large (0.25–0.50 mm) eggs, in a pair of saucer-shaped ovigerous lamellae held in the bottom of the mantle cavity by a pair of ovigerous fraena, were found in three of the five individuals examined internally; embryos from one individual consisted of nauplii with well-developed appendages and caudal spines, but whether they are released as feeding or non-feeding nauplii, or as cyprids, remains unknown.

#### JUVENILE STAGES

A number of ontogenetic stages following cyprid metamorphosis were found attached primarily to established hermaphrodites (adults), and, as noted above, they will be described in more detail elsewhere (Newman 1989). Juveniles found on adults were most commonly attached along the articulation between the tergum and scutum of either side (Fig. 1A), a position where they receive protection from the adults when crowded, and a position that could be advantageous should they develop precociously as males (*see* Charnov 1987 and Klepal 1987).

Following cyprid metamorphosis, juveniles pass through several pedunculate stages, and those developing on the surface of adults orient in the same direction as the adult before undergoing metamorphosis into sessile juveniles. If a sessile juvenile is attached to the right side of an adult, its movable side will be the right side, but if it settles on

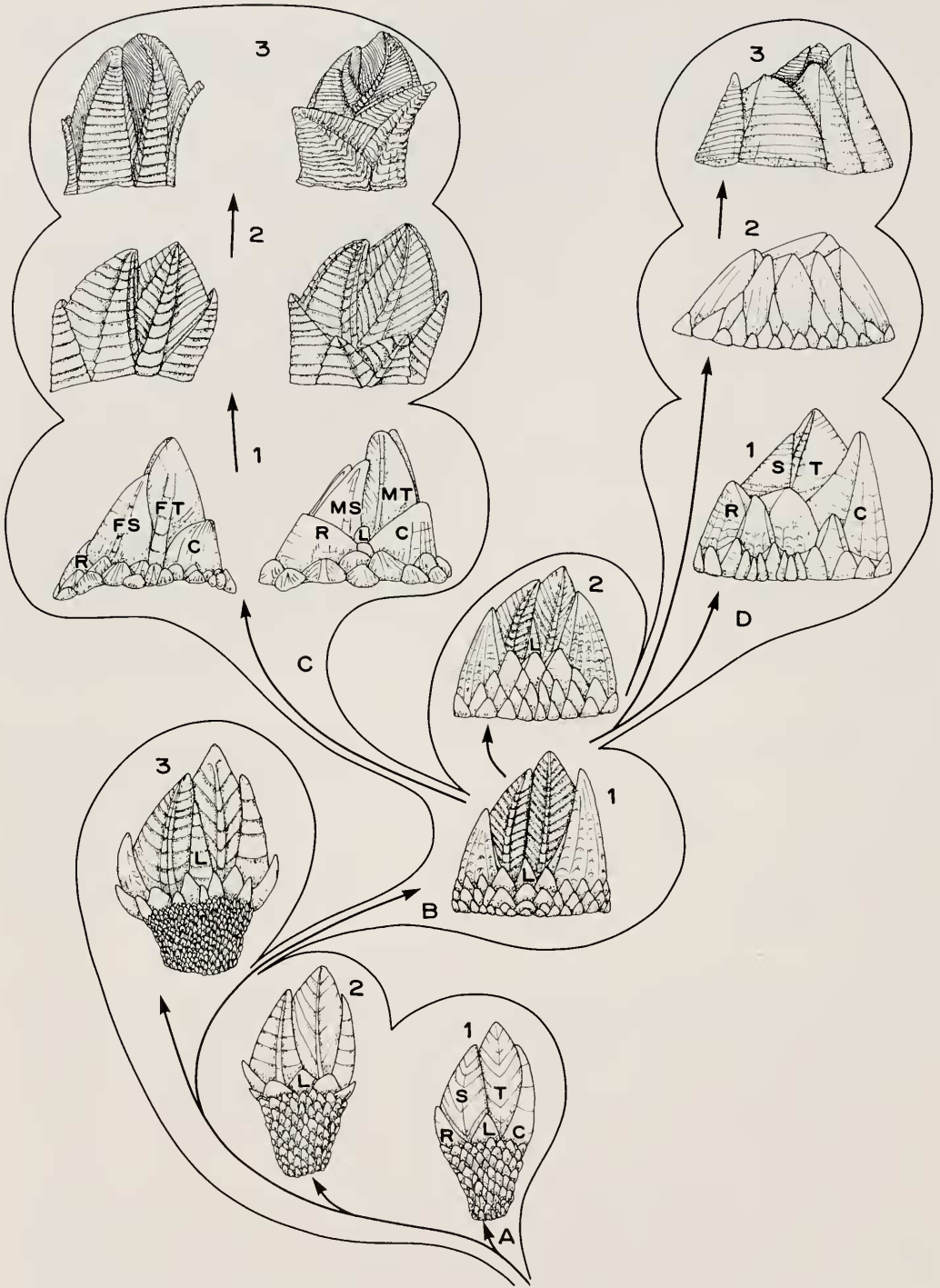


FIGURE 4. Origin and radiation of the sessile barnacles. The four major radiations in this diagram are distinguished by major evolutionary innovations: A, the development of a complex capitular armament, by transfer of peduncular plates to the capitulum, in scalpellomorphans Pedunculata (note three latera in A-2 between R and C); A to B, advent of the Sessilia or sessile barnacles (Brachylepadorpha) by elimination of the peduncle and further development of a modest separation between an operculum and the remaining capitular plates (note that three tiers of latera close the gap between rostrum and carina); B to C, divergence of the asymmetrical sessile barnacles, Verrucomorpha, by fixation of S and T (FS and FT) between R and C of one side, the joining of R and C to support S and T (MS and MT) of the movable side, and the subsequent



the left side of the adult, its movable side will be the left side. Thus, right or left sidedness is ecotypically determined, and this is likely the case in other verrucomorphans in which right and left sidedness occurs in the same species.

The peduncle is naked in the pedunculate juvenile stages, and, in the earliest, the capitular plates are symmetrically arranged, all as in the early juveniles of scalpellomorphans. Capitular asymmetry gradually becomes evident through differential appearance and growth of the plates and the heterochronous appearance of the first whorl of latera before the median latus on the incipient movable side. When the essential transformations heralding the verrucomorphan asymmetry are completed, the last pedunculate juvenile undergoes an abrupt metamorphosis into the first sessile juvenile. While distinct pedunculate stages are unknown in the ontogeny of other sessile barnacles, Darwin (1854) noted the semblance of a peduncle during metamorphosis from the cyprid to the first juvenile in *Semibalanus balanoides*.

## SYSTEMATICS

Subclass Cirripedia Burmeister, 1834

Superorder Thoracica Darwin, 1854, ?Cambrian, Silurian–Recent

Order Sessilia, Upper Mesozoic–Recent

Suborder Verrucomorpha Pilsbry, 1916 (amended)

Asymmetrical sessile barnacles, the primary walls of which consist of a chamber formed by the rostrum and carina abutting on one side and a scutum and tergum interposed and fixed between them on the opposite or “fixed” side, and closed by the movable scutum and tergum or operculum (Darwin 1854, *Verruca sensu lato*, see Fig. 4C-3 herein); the wall is sometimes provided with a pair of latera (rostro- and carinolatus) on the movable side (Withers 1914b, *Eoverruca* and *Proverruca*, see Fig. 4C-2 herein), or it is surrounded by several basal whorls of small, imbricating plates elevating the principal wall plates above the substratum and includes a median latus interposed between the scutum and tergum of at least the movable side (Fig. 4C-1, *Neoverruca* gen. nov.).

As can be seen from this diagnosis, and as depicted in Fig. 4C, the verrucomorphans fall into three natural groups, beginning with the new form (superficially indistinguishable from the Brachylepadomorpha) and ending with the familiar and highly modified form on which the suborder was founded (*Verruca* s. l., including allied genera listed

---

loss of all latera, bringing the principal wall plates into contact with the substratum; B to D, divergence of the higher symmetrical sessile barnacles, the Balanomorpha, by closing of the gap on both sides, between R and C, with a few enlarged and specialized latera and, concomitantly, by bringing R and C and the principal latera into contact with the substratum. The median latus (L) was known to go with the operculum in brachylepadomorphs, it is now known to do likewise in the verrucomorphs; and it was inferred to do so in the primitive balanomorphan, *Catophragmus* (see Newman 1987). However, the homologies of the latera of a very primitive balanomorphan, *Chionelasmus* (Fig. 4D-1) remain conjectural.

A, Pedunculata; relevant Scalpellomorpha, A-1, *Neolepas zeviniae* from hydrothermal vents at 2600 m, Eastern Pacific; A-2, *Scillaelepas*, a deep-sea amphitropical complex, 400–2000 m; and A-3, *Capitulum mitella*, intertidal, ?Madagascar–Western Pacific. B, C, and D, Sessilia. B, †Brachylepadomorpha, Europe, North America, and Antarctica; B-1, generalized brachylepadomorphan; B-2, †*Brachylepas cretacea*,\* England. C, Verrucomorpha;\*\* C-1, *Neoverruca brachylepadoformis* gen. et sp. nov., small (1.0 cm high) uncrowded individual from 3600 m, hydrothermal springs, Mariana Back-Arc Basin (ALV Sta. 1840); C-2, †*Eoverruca hewitti*, England; and C-3, *Verruca*, cosmopolitan, mostly deep water to approximately 5000 m. D, Balanomorpha; D-1, *Chionelasmus darwini*, deep water (approximately 500 m), islands of the Indo-West Pacific; D-2, generalized *Catophragmus* s. l.,\* extant species, intertidal, Bermuda and Caribbean islands, offshore islands on the Pacific side of Panama and Costa Rica, and Southeast Australia and Tasmania; D-3, Bathylasmatidae (*Hexelasma*), Western Atlantic and Western Pacific, deep water, 100–3000 m.

†, Extinct; \*, unessential basal imbricating plates toward rostral and carinal ends omitted; \*\*, asymmetry in verrucomorphans can be either right or left sided in the same population. For ease of comparison between sides of these verrucomorphans, all side views are illustrated as though they were of the right side. C, carina; FS, fixed scutum; FT, fixed tergum; L, median latus; MS, movable scutum; MT, movable tergum; R, rostrum; S, scutum; and T, tergum (A, B, and D-1–2 from Newman 1987, C-2 modified from Withers 1935, C-3 modified from Pilsbry 1916, and D-3 from Hoek 1913).

below under the Verrucidae; see Zevina 1987b). Since this evolutionary sequence has been achieved by reduction, it is possible that some members of *Verruca* s. l. have descended more than once from the proverrucan and/or the neoverrucan level of organization. However, there is presently no morphological evidence for convergence at any level within the Verrucomorpha. Therefore we propose that these three groups be recognized at the family-group level, as follows, in order of increasing specialization:

**Neoverrucidae** Newman, fam. nov. The primary wall is elevated above the substratum by basal whorls of imbricating plates, and a median latus is interposed between the movable scutum and tergum (Recent, unless some fossils, particularly some already attributed to the Brachylepadomorpha, prove to be neoverrucids). *Neoverruca* gen. nov.

**Proverrucidae** Newman, fam. nov. The primary wall is in contact with substratum and is provided with two overlapping latera protecting the rostro-carinal suture on the movable side (Upper Cretaceous). *Proverruca* Withers, 1914b; family includes *Eoverruca* Withers, 1935.

**Verrucidae** Darwin, 1854. The primary wall is in contact with the substratum and is without latera of any sort (?Middle, Upper Cretaceous–Holocene). The genus *Verruca* s. l. proved to be species-rich with the advent of deep-sea explorations, and a number of subgenera, presumably representing natural groups, have been erected. Zevina (1987a, b) has proposed that the subgenera be elevated to full generic rank. To these she added a new genus, and the six are listed below more or less in order of increasing specialization:

- (1) *Altiverruca* Pilsbry, 1916:40 (Type: *V. hoeki* Pilsbry, 1907; ? = *V. gibbosa* Hoek, 1883; Zevina 1987b:1813).
- (2) *Verruca* Schumacher, 1817:35 (Type: *Lepas stroemia* Müller, 1776).
- (3) *Cameraverruca* Pilsbry, 1916:39 (Type: *V. euglypta* Pilsbry, 1907).
- (4) *Metaverruca* Pilsbry, 1916:21 (Type: *V. coraliophila* Pilsbry, 1916).
- (5) *Rostratoverruca* Broch, 1922:297 (Type: *V. nexa* Darwin, 1854).
- (6) *Spongoverruca* Zevina, 1987b:1813 (Type: *V. spongicola* Gruvel, 1911).

While derived characters are generally used to distinguish among several of these genera, *Altiverruca* and *Verruca* sensu stricto are distinguished primarily on the basis of whether the plane of the movable plates is nearly vertical or horizontal to the substratum. In light of the variation observed in *Neoverruca* in this regard, the possibility that some species included in these genera express comparable ecophenotypic variability exists, and therefore the distinction between these two otherwise unspecialized genera should probably be viewed with caution.

The relationships of the Verrucomorpha to the symmetrical sessile barnacles, and the radiation of the latter, are illustrated in Figure 4, while times of first appearance and geologic ranges are depicted in Figure 5.

#### DISCUSSION AND CONCLUSIONS

*Biogeographical and evolutionary significance.*—Both hydrothermal barnacles, *Neolepas* from the East Pacific and *Neoverruca* from the West Pacific, are of evolutionary significance because they are the most primitive living members of their lineages, the pedunculate Scalpellomorpha and sessile Verrucomorpha (Fig. 4A-1 and C-1, respectively). It is also biogeographically significant that these two ancient “Mesozoic” morphologies are found today as relics in the refugium provided by abyssal hydrothermal springs. Thus, the discovery of *Neoverruca* not only further falsifies the hypothesis that the Brachylepadomorpha and Verrucomorpha rose independently from scalpellomorph ancestors (see Newman 1987), it further falsifies the hypothesis that vents and cognate environments are inhabited by rapidly evolving recent immigrants (see Newman 1985).

*Neoverruca*, in having a verrucomorphan facies superimposed on a brachylepadomorph ground plan, represents a “missing link” as well as a “living fossil” relevant to the early evolution of the sessile barnacles. *Neoverruca* is furthermore remarkable

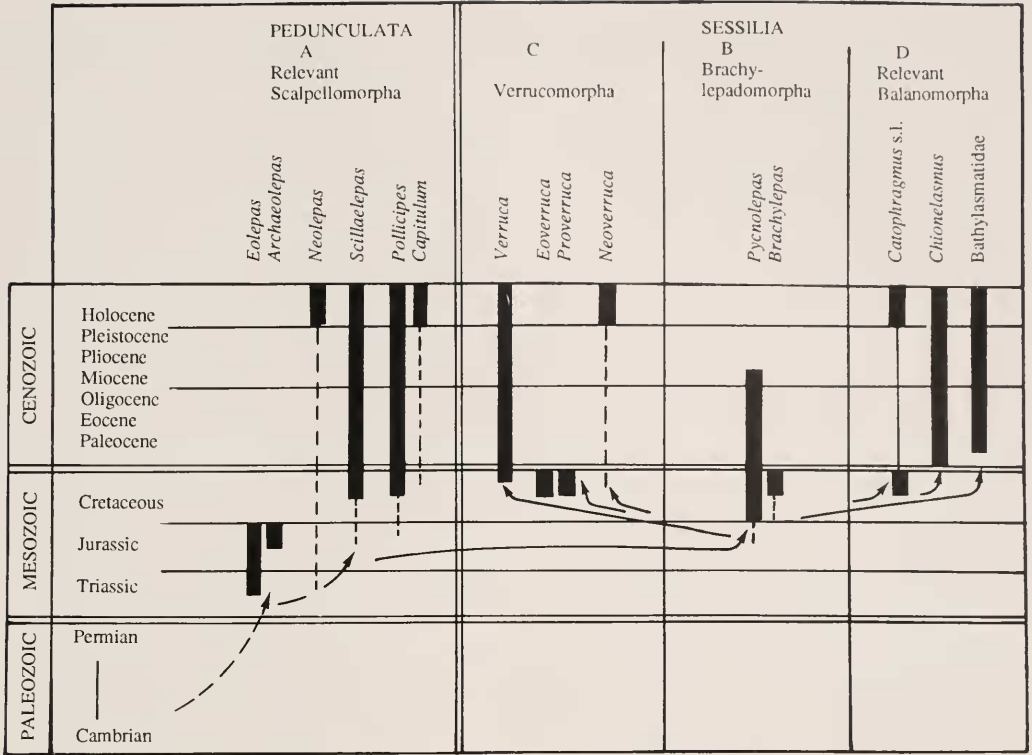


FIGURE 5. Geological ranges of the principal sessile barnacles and their ancestral pedunculate lineage. Of the three lineages of sessile barnacles, (1) all appear in the Cretaceous; (2) the earliest, the Brachylepadomorpha, went extinct, but its organization plan was central to the evolution of the higher forms; (3) the Verrucomorpha, including the most primitive living sessile barnacle, *Neoverruca*, is moderately diverse although presently confined almost exclusively to the deep sea; and (4), the Balanomorpha, including the oldest surviving members *Catophragnus* s. l. and *Chionelasmus*, having a relict intertidal distribution and a moderately deep-water Indo-West Pacific relic distribution, respectively, has a substantial diversity primarily in shallow water (Newman and Stanley 1981).

Solid vertical bars represent the ranges of genera; the gap in the bar under *Catophragnus* s. l. probably reflects the fact that intertidal Balanomorpha are less frequently encountered in the fossil record than are shallow-water forms. However, the Cretaceous form appears only remotely related to the Recent forms which, in themselves, represent three morphologically very distinct and geographically isolated populations (Stanley and Newman 1980). The dashed vertical lines indicate inferred ranges, and the extensive range for *Neolepas*, initially justified on theoretical grounds, has been corroborated by a tentative identification of its morphology in the Triassic of New Caledonia (Buckeridge and Grant-Mackie 1985). While the thoracican cirripeds may stem from the Cambrian (Collins and Rudkin 1981; but see Briggs 1983), the oldest potential relatives of the scalpellomorphan pedunculates are the Carboniferous praelepadids and, therefore, the dashed arrow directed toward the earliest Mesozoic scalpellomorphs can be inferred to stem from them (Newman *et al.* 1969, Newman 1987).

in passing through a number of pedunculate juvenile stages during ontogeny. Therefore, knowledge of *Neoverruca* provides insights not only into the affinities between symmetrical and asymmetrical sessile barnacles, but into their pedunculate ancestors as well, and then beyond what analyses of extant pedunculate barnacles have been able to provide.

*The origin of symmetrical sessile barnacles.*—As Darwin (1854) noted, the symmetrical sessile barnacles differ from their ancestral scalpellomorphan prototype in a number of features, the most obvious being the conversion of the peduncle into a flat, membranous basis extending across the perimeter of the capitulum and cementing it to the substratum. Other more or less concomitant advances included (1) specialization of two or more pairs of latera in closing the gap on each side between the rostrum and carina and, ultimately, their complete integration into the wall in higher forms, (2)

development of a distinctly separate, movable operculum and its subsequent specializations, (3) eventual elimination of the remaining, undedicated basal imbricating plates and, finally, (4) reduction of the number of latera making up the primary wall (Fig. 4B, D-1-3).

There also were a number of changes within the mantle cavity in the course of evolution from the pedunculate to the symmetrical mode. Two important ones involved the loss of the ovigerous fraena, setose devices holding the eggs in place, and the loss of filamentary appendages, strap-like organs presumably used in respiration. Filamentary appendages were replaced by branchiae in balanomorphs (Darwin 1854) and, while higher balanomorphs have branchiae alone, Walker (1983) discovered that the primitive balanomorph *Catophragmus* has both fraena and branchiae. On the other hand, while higher verrucomorphans were presumed to have lost fraena and filamentary appendages, they apparently never developed branchiae. It is noteworthy that *Neoverruca*, the first sessile barnacle known to have ovigerous fraena and a filamentary appendage, satisfies this expectation; in fact, this must also have been the condition in brachylepadomorphans because it is the condition in some surviving members of the pedunculate lineage that gave rise to them.

*Catophragmus* (Fig. 4D-2) was the most primitive sessile barnacle known to Darwin (1854), and he treated it as a model elucidating transitional features between pedunculate barnacles like *Pollicipes* and *Capitulum* and the higher sessile barnacles. Subsequently, two extinct sessile barnacles (*Brachylepas* Woodward, 1901, and the somewhat more primitive *Pycnolepas* Withers, 1914*b*; see Fig. 4B herein) replaced *Catophragmus* as the most primitive forms. However, despite Woodward's and Withers' considerations to the contrary, Pilsbry (1907) pronounced that the arrangement of imbricating plates in the *Brachylepas* and *Catophragmus* was basically different and that the two lineages had likely arisen independently from pedunculate ancestors. However, a recent study of the imbricating system in *Brachylepas cretacea* (see Newman 1987), including an analysis of the principal latera as viewed from within as well as from without, revealed how the arrangement of latera seen in balanomorphs could have been attained through loss and rearrangement of certain of the principal latera in a *Brachylepas*-like ancestor. The phylogenetic inferences so derived, including the transfer of the median latus to the operculum in the evolution of *Catophragmus*, called for rejection of polyphyly in favor of monophyly in the evolution of the symmetrical sessile barnacles (Newman 1987). Knowledge of the basically brachylepadomorphan organization of *Neoverruca*, and the presence of pedunculate stages in its ontogeny, does much to further our understanding of how this transition took place.

*The origin of the asymmetrical sessile barnacles.*—Understanding of the origin of verrucomorphans has been clouded by conjecture since Darwin (1854). He spent much of his time on *Verruca* s. l., morphologically the most specialized of the verrucomorphans as we know them today, in working out homologies of the plates with those of scalpellomorphan and balanomorphan barnacles and in trying to decide whether the unique organization plan (Fig. 4C-3) had pedunculate or sessile antecedents. While ambivalent throughout most of his deliberations, Darwin did state that if compelled he would with much hesitation place *Verruca* closer to the sessile than to the pedunculate barnacles.

On the other hand, following the discovery of the first living representative of the pedunculate barnacles, *Scillaelepas*, and the primitive verrucid having two pairs of somewhat similarly deployed latera, *Proverruca* (Fig. 4A-2 and C-2, respectively), Pilsbry (1916) accepted a pedunculate origin for the verrucids and proposed a new suborder, the Verrucomorpha. Shortly thereafter, it was discovered that fossil material previously thought by Darwin and others to represent *Pollicipes* s. l. constituted a new sessile genus, *Pycnolepas*, related to but more primitive than *Brachylepas*. This led to the creation of a third independent suborder of sessile barnacles, the Brachylepadomorpha (Withers 1923; see Fig. 4B herein) and to the notion of a triphyletic origin of the sessile barnacles that became the dogma that all workers followed (Krüger 1940, Withers 1953, Newman *et al.* 1969, Newman and Ross 1976, Newman 1982). However, as noted above, compelling evidence for independent pedunculate origins for the Brachy-

lepadomorpha and Balanomorpha is lacking; to the contrary, by loss and rearrangement of the latera it is quite apparent how the latter could have been derived from the former (Newman 1987). And now the structure of the new form, *Neoverruca*, clearly illustrates the brachylepadomorphan origin of the Verrucomorpha and falsifies the hypothesis of even a diphyletic origin of the sessile barnacles involving these two lineages.

*Neoverruca* displays, in a subtle way, the profound initial morphological adjustments made in the shell of a *Brachylepas*-like ancestor that led to the development of the unique wall and operculum of the asymmetrical sessile barnacles. Such adjustments are most readily made when the latera involved have not become an integral, dedicated part of the primary wall, and their being readily excludable allowed one half of the brachylepadomorphan operculum to be incorporated into the primary wall of the verrucomorphan. This remarkable adjustment is rendered comprehensible when it is noted that it involves the barnacle's leaning to one side or the other during ontogeny. The adaptive value of leaning over, in an otherwise relatively high sessile barnacle, becomes obvious if the development following settlement of a young barnacle in a crowded colony is followed; leaning over allows young individuals to extend their cirri upward and outward, in the same direction as those of the adults on which they settled (Newman 1989). It is evident that this initially small adjustment, of letting the scutum and tergum of one side come down between the rostrum and carina during ontogeny, set the stage for the remarkable divergence of the asymmetrical from the symmetrical forms early in the evolutionary radiation of the sessile barnacles.

Finally, it should be noted that while Withers (1914*b*) considered the latera of proverrucids to be the rostro- and carino-latera (RL/CL) of a *Scillaelepas*-like ancestor, Newman (1987) concluded they were as likely to be the rostro- and median latera (RL/L). However, we now know that the median latus goes with the operculum in neoverrucids, and therefore it cannot be one of the wall latera in proverrucids. Furthermore, from knowledge of the ontogeny of *Neoverruca* (Newman 1989), it is apparent that the evolutionary transition from a neoverruca to the proverrucid wall must have involved progenesis (curtailment of whorl production following the formation of the first whorl). Therefore, since it appears ontogenetically and progenetically impossible for the latera in proverrucids to be plates from any of the subsequent whorls, they must be RL/CL, as Withers had proposed.

*Pedunculate ancestors of the sessile barnacles.*—The most primitive living scalpellomorph is the hydrothermal barnacle *Neolepas*. It has simple capitular armament including but one pair of latera (Fig. 4A-1). A more advanced form, *Scillaelepas*, abundant in shallow water in the Cretaceous but presently represented by a dozen or so species living only in the deep sea, has added two more pairs of latera, a subcarina, and sometimes one or more subrostra (Fig. 4A-2; Newman 1980). More advanced and ordinarily intertidal forms, the Tethyan relict *Pollicipes* and the Indo-West Pacific relict *Capitulum* (Fig. 4A-3), have several additional whorls of smaller latera around the base of the capitulum. There has been a long-standing consensus that the sessile barnacles evolved from the scalpellomorph lineage represented by these genera (Darwin 1854, Woodward 1901; Newman *et al.* 1969; Ghiselin and Jaffe 1973; Anderson 1983; Newman 1982, 1987). The existence and nature of the pedunculate stages in the ontogeny of the most primitive living sessile barnacle (Newman 1989), *Neoverruca*, illustrate that the Darwinian/Woodwardian model for the pedunculate ancestry of the sessile barnacles is well founded.

#### ACKNOWLEDGMENTS

We would like to acknowledge the constructive criticism and advice of two anonymous referees.

#### ADDENDUM

What is apparently the most primitive living balanomorphan, fitting between B and D-1 in Figure 4 herein, has been recently recovered by Japanese scientists from an abyssal hydrothermal spring at approximately 2000 m in the North Fiji Basin (Toshiyuki Yamaguchi, *personal communication*).

## LITERATURE CITED

- Anderson, D. T. 1980. Cirral activity and feeding in the verruciform barnacles *Verruca recta* Aurivillius and *V. stroemia* (O. F. Müller) (Cirripedia). *Journal of the Marine Biological Association of the United Kingdom* 60:348–366.
- Anderson, D. T. 1983. *Catomerus polymerus* and the evolution of the balanomorph form in barnacles (Cirripedia). *Memoirs of the Australian Museum* 18:7–20.
- Anderson, D. T., and A. J. Southward. 1987. Cirral activity of barnacles. Pp. 135–174 in A. J. Southward (ed.). *Barnacle Biology, Crustacean Issues* 5. Balkema, Rotterdam.
- Briggs, D. E. G. 1983. Affinities and early evolution of the Crustacea: The evidence of the Cambrian fossils. Pp. 1–22 in F. R. Schram (ed.). *Crustacean Phylogeny, Crustacean Issues* 1. Balkema, Rotterdam.
- Broch, H. 1922. Papers from Dr. Th. Mortensen's Pacific Expedition, 1914–16. X. Studies on Pacific Cirripedes. *Videnskabelige meddelelser fra Dansk Naturhistorisk Forening i København* 73:215–358.
- Buckeridge, J. S. 1983. Fossil barnacles (Cirripedia: Thoracica) of New Zealand and Australia. *New Zealand Geological Survey Paleontological Bulletin* 50:1–151 + pls. 1–13.
- Buckeridge, J. S., and J. A. Grant-Mackie. 1985. A new scalpellid barnacle (Cirripedia; Thoracica) from the Lower Jurassic of New Caledonia. *Géologie de la France* (1):77–80.
- Charnov, E. L. 1987. Sexuality and hermaphroditism in barnacles: A natural selection approach. Pp. 89–104 in A. J. Southward (ed.). *Barnacle Biology, Crustacean Issues* 5. Balkema, Rotterdam.
- Collins, D., and D. M. Rudkin. 1981. *Priscanserminarius barnetti*, a probable lepadomorph barnacle from the Middle Cambrian Burgess Shale of British Columbia. *Journal of Paleontology* 55:1006–1015.
- Collins, J. S. H. 1980. A new *Pycnolepas* (Cirripedia) from the (?) Lower Aptian of Alexander Island. *British Antarctic Survey Bulletin* No. 50:21–26.
- Darwin, C. R. 1854. A monograph on the sub-class Cirripedia, with figures of all species. The Balanidae, &C. 684 pp. + pls. 1–30. Ray Society, London.
- Ghiselin, M. T., and L. Jaffé. 1973. Phylogenetic classification in Darwin's monograph on the sub-class Cirripedia. *Systematic Zoology* 22: 132–140.
- Hessler, R. R., and W. M. Smithey, Jr. 1983. The distribution and community structure of megafauna at the Galapagos Rift hydrothermal vents. Pp. 735–770 in P. A. Ronds, K. Bostrom, and K. L. Smith, Jr. (eds.). *Hydrothermal Processes at Seafloor Spreading Centers*. Plenum, New York.
- Hessler, R. R., P. Lonsdale, and J. Hawkins. 1988. Patterns on the ocean floor. *New Scientist* No. 1605:47–51.
- Hoek, P. P. C. 1883. Report on the Cirripedia collected by H.M.S. Challenger during the years 1873–1876. *Reports on Scientific Research: Zoology* 8(25):1–169 + pls. 1–13.
- Hoek, P. P. C. 1913. Cirripedia of the Siboga-Expedition: B. Cirripedia Sessilia. *Siboga-Expedition* 21:129–275 + pls. 11–27. Brill, Leyden.
- Jones, M. L. (ed.). 1985. The Hydrothermal Vents of the Eastern Pacific: An Overview. *Bulletin of the Biological Society of Washington*, No. 6, 566 pp.
- Killingley, J. S., and W. A. Newman. 1982.  $^{18}\text{O}$  fractionation in barnacle calcite: A barnacle paleotemperature equation. *Journal of Marine Research* 40:893–902.
- Klepál, W. 1987. A review of the comparative anatomy of the males of cirripedes. *Oceanography and Marine Biology Annual Reviews* 25: 285–351.
- Krüger, P. 1940. Cirripedia. *H. G. Bronns Klassen und Ordnungen des Tierreichs* 5 (1, 3, 3):1–145. Leipzig.
- Newman, W. A. 1979. A new scalpellid (Cirripedia); a Mesozoic relic living near an abyssal hydrothermal spring. *Transactions of the San Diego Society of Natural History* 19:153–167.
- Newman, W. A. 1980. A review of extant *Scillae* (Cirripedia: Scalpellidae) including recognition of new species from the North Atlantic, Western Indian Ocean and New Zealand. *Tethys* 9:379–398.
- Newman, W. A. 1982. Cirripedia. Pp. 197–221 in L. Abele (ed.). *The Biology of Crustacea*, Vol. 1. Academic Press, New York.
- Newman, W. A. 1985. The abyssal hydrothermal vent invertebrate fauna: A glimpse of antiquity? Pp. 231–242 in M. L. Jones (ed.). *The Hydrothermal Vents of the Eastern Pacific: An Overview*. *Bulletin of the Biological Society of Washington*, No. 6.
- Newman, W. A. 1987. Evolution of Cirripedes and their major groups. Pp. 3–42 in A. J. Southward (ed.). *Barnacle Biology, Crustacean Issues* 5. Balkema, Rotterdam.
- Newman, W. A. 1989. Juvenile ontogeny and metamorphosis in the most primitive living sessile barnacle, *Neoverruca*, from abyssal hydrothermal springs. *Bulletin of Marine Science*, in press.
- Newman, W. A., and A. Ross. 1976. Revision of the balanomorph barnacles; including a catalogue of the species. *Memoirs of the San Diego Society of Natural History* 9:1–108.
- Newman, W. A., and S. M. Stanley. 1981. Competition wins out overall: Reply to Paine. *Paleobiology* 7:561–569.
- Newman, W. A., V. A. Zullo, and T. H. Withers. 1969. Cirripedia. Pp. R206–295 in R. C. Moore (ed.). *Treatise on Invertebrate Paleontology*, Part R, Arthropoda 4, Vol. 1. University of Kansas and the Geological Society of America, Boulder.
- Pilsbry, H. A. 1907. The barnacles (Cirripedia) contained in the collections of the U.S. National Museum. *Bulletin of the U.S. National Museum* 60:1–122 + pls. 1–11.
- Pilsbry, H. A. 1916. The sessile barnacles (Cirripedia) contained in the collections of the U.S. National Museum. *Bulletin of the U.S. National Museum*. *Bulletin of the U.S. National Museum*.

- States National Museum 93:1-366 + pls. 1-76.
- Schumacher, H. C. F. 1817. Essai d'un nouveau système des habitations des Vers testaces, &c. 287 pp. + 22 pls. Copenhagen.
- Stanley, S. M., and W. A. Newman. 1980. Competitive exclusion in evolutionary time: The case of the acorn barnacles. *Paleobiology* 6: 173-183.
- Udvardy, M. D. F. 1969. *Dynamic Zoogeography with Special Reference to Land Animals*. Van Nostrand Reinhold, New York.
- Walker, G. 1983. A study of the ovigerous fraena of barnacles. *Proceedings of the Royal Society, London B* 218:425-442.
- Withers, T. H. 1914a. Some Cretaceous and Tertiary cirripedes referred to *Pollicipes*. *Annals and Magazine of Natural History, Ser. 8*, 14: 167-206 + pls. 7 and 8.
- Withers, T. H. 1914b. A remarkable new cirripede from the chalk of Surrey and Hertfordshire. *Proceedings of the Zoological Society of London*, No. 64:945-953.
- Withers, T. H. 1923. Die Cirripeden der Kreide Rügens. *Abhandlungen aus dem geologisch palaeontologischen Institut der Universität Greifswald* 3:1-54 + 3 pls.
- Withers, T. H. 1935. *Catalogue of Fossil Cirripedia in the Department of Geology*. 2 (Cretaceous):1-535 + pls. 1-50. British Museum (Natural History), London.
- Withers, T. H. 1953. *Catalogue of Fossil Cirripedia in the Department of Geology*. 3 (Tertiary):1-396 + pls. 1-64. British Museum (Natural History), London.
- Woodward, H. 1901. On "*Pyrgoma cretacea*," a cirripede from the Upper Chalk of Norwich and Margate. *The Geological Magazine, New Series, Decade IV* 8:145-152 + pl. 8.
- Zevina, G. B. 1987a. Abyssal Cirripedia Verrucomorpha (Thoracica) of the Atlantic and Indian Ocean. *Zoologicheskyy Zhurnal* 66:1304-1313.
- Zevina, G. B. 1987b. Deep-sea Verrucomorpha (Cirripedia, Thoracica) of the Pacific: 1. The North Pacific. *Zoologicheskyy Zhurnal* 66:1812-1821.
- Zevina, G. B. 1988. Deep-sea Verrucomorpha (Cirripedia, Thoracica) of the Pacific: 2. The South Pacific. *Zoologicheskyy Zhurnal* 67:31-40.
- Zullo, V. A., E. E. Russell, and F. F. Mellen. 1987. *Brachylepas* Woodward and *Virgiscalpellum* Withers (Cirripedia) from the Upper Cretaceous of Arkansas. *Journal of Paleontology* 61: 101-111.